

Morphological and molecular characterizations of *Myxobolus tachysurus* sp. nov. (Myxozoa, Myxosporea) infecting the palate of yellow catfish *Tachysurus fulvidraco* in China

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<https://zoobank.org/16B69A36-A136-4026-89D7-6397CB6C2E3F>

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Academic editor: Pavel Stoev ♦ Received 12 December 2025 ♦ Accepted 20 January 2026 ♦ Published 12 February 2026

Abstract

The Xiangjiang River, a major tributary of the Yangtze River and the largest river in Hunan Province, harbors approximately 179 fish species. As part of an ongoing survey of myxosporean diversity in this river, a new *Myxobolus* species infecting the yellow catfish *Tachysurus fulvidraco* was discovered. The new species was characterized based on morphological, histopathological, infection-related, and molecular analyses. Macroscopic whitish plasmodia were formed in the muscle layer of the palate, with no distinct inflammatory reaction observed. Morphological comparisons revealed that this species can be distinguished from morphologically similar species by differences in plasmodial size, myxospore size, and polar capsule size, as well as by infection sites and the number of polar tube coils. Phylogenetic analyses indicated that species clustered mainly according to host affinity, with few exceptions. The novel species did not cluster with Siluriformes-infecting species with pyriform myxospores within Clade D. Instead, it formed a sister clade to *M. separatus*, which infects the gill filaments of *T. fulvidraco*, and *M. nagaraensis* within Clade A, with moderate support values. Based on these findings, the parasite is described herein as a new species, *Myxobolus tachysurus* sp. nov.

Key Words

Myxobolus tachysurus sp. nov., Myxozoa, palate, *Tachysurus fulvidraco*

Introduction

Myxozoa, a significant metazoan parasite with a cnidarian ancestor, infects various organs and tissues in both invertebrates, such as annelids, and vertebrates, primarily fish, but also birds, reptiles, amphibians, and mammals (Lom and Dyková 2006; Yokoyama et al. 2012; Fiala et al. 2015; Holzer et al. 2018). Currently, more than 3000 species have been described globally, with nearly half belonging to the genus *Myxobolus* Bütschli, 1882. Species of *Myxobolus* are characterized by having two equal or unequal polar capsules at the anterior end, pyriform, oval, or ellipsoidal myxospores, and a distinct iodophilous

vacuole (Eiras et al. 2005; Eiras et al. 2014; Eiras et al. 2021). In China, around 400 *Myxobolus* species have been reported previously (Chen and Ma 1998; Eiras et al. 2014; Eiras et al. 2021). Most of them were described from various organs across diverse hosts, contradicting the established tissue tropism and host specificity of Myxozoa, as demonstrated by researchers, and leading to the recognition of many synonyms or cryptic species (Chen and Ma 1998). In recent years, researchers in China have conducted numerous surveys to identify previously undocumented species and discover new species (Liu et al. 2012; Zhang 2023; Zhao et al. 2023). While most species were harmless to their hosts, some caused

severe myxosporidiosis, leading to significant fish mortality (Zhang et al. 2010; Liu et al. 2012; Zhao et al. 2013 2023; Zhang 2023). These species include pharyngeal myxosporidiosis caused by *Myxobolus honghuensis* Liu, Whipps, Gu, Zeng & Huang, 2012 from *Carassius auratus gibelio* Bloch, 1782; *Myxobolus wulii* Landsberg & Lom, 1991 infecting the liver of *C. auratus gibelio*; and *Myxobolus ampullicapsulatus* Zhao, Sun, Kent, Deng & Whipps, 2008 infecting the gills of *Carassius auratus auratus* Linnaeus, 1758 (Zhang et al. 2010; Liu et al. 2012; Zhao et al. 2013).

The Xiangjiang River is the largest tributary of the Yangtze River in Hunan Province. Its mainstream extends 969 kilometers and encompasses a drainage area of 94,660 square kilometers. It harbors approximately 179 fish species from 96 genera, 28 families, and 13 orders (Wu et al. 2021). Despite this richness, information on the diversity of fish myxosporeans in the Xiangjiang River remains limited. Only two surveys of myxosporean infections, reporting 58 species belonging to seven genera, including *Myxobolus*, *Thelohanellus*, *Henneguya*, *Myxidium*, *Zschokkella*, *Chloromyxum*, and *Sphaerospora*, have been conducted previously (Jin et al. 1993; Liu 2015). To expand knowledge of myxozoan diversity, we conducted a survey of myxosporean infections in fishes of the Xiangjiang River. During this study, a new *Myxobolus* species infecting the palate of the yellow catfish *Tachysurus fulvidraco* Richardson, 1846, was identified and characterized using morphological, histopathological, and molecular analyses.

Materials and methods

Morphological examination

From June 2020 to July 2023, forty-four specimens of yellow catfish, *Tachysurus fulvidraco*, with body weights ranging from 90.8 to 110.4 g, were randomly collected using a gill net in the Xiangjiang River, located in Changsha City, Hunan Province, China (28°18'58"E, 112°54'4"N). The specimens were promptly removed from the net and transported to the local Fish Diseases Laboratory. A thorough examination of various organs, including the gills, skin, fins, liver, and gallbladder, was performed to detect suspected plasmodia, either visually or using a Motic SMZ161 dissecting microscope (Motic, China). Upon detection, plasmodia samples were prepared as microscope slides for further examination using a Novel NE910 light microscope (Novel, China). Subsequently, infected tissues and isolated plasmodia were preserved in 10% neutral buffered formalin for histopathological analysis and in 70% ethanol for molecular analysis. Photographs of fixed spores were captured using an Olympus BX53 microscope (Olympus, Japan) at 400× magnification, equipped with an MSX 11 digital camera (Mingmei, China). Morphological characteristics of spores and plasmodia were obtained from the digital images, following the guidelines outlined by Lom and Arthur (1989).

Measurements were recorded as means $\pm$ standard error (range). Schematic illustrations of myxospores were created using CorelDraw X6 software (Corel, Ottawa, Canada) based on the captured photographs.

Histopathological examination

Initially, infected tissues were fixed in 10% neutral buffered formalin for 24 hours. The tissues were then dehydrated through a graded series of ethanol solutions, embedded in paraffin wax, sectioned at a thickness of 5–6 μ m, stained with hematoxylin and eosin (H&E), and examined and photographed under light microscopy.

DNA isolation and sequencing

Infected tissues stored in 70% ethanol were subjected to DNA extraction using a Qiagen DNeasy Blood & Tissue Kit (Qiagen, Germany). Partial nuclear 18S rDNA gene sequences were amplified using the primers MyxospecF (5'-TTCTGCCCTATCAACTWGTTG-3') (Fiala 2006) and 18R (5'-CTACGGAAACCTTGTTACG-3') (Whipps et al. 2003). Polymerase chain reaction (PCR) amplification was performed in a 25 μ L reaction mixture containing 1 μ L of extracted template DNA, 1 μ L of each primer, 12.5 μ L of 2× Rapid Taq MasterMix (Vazyme Biotech, China), and 9.5 μ L of double-distilled water (ddH₂O). Thermocycler conditions consisted of an initial denaturation at 94 °C for 4 minutes, followed by 35 cycles of 94 °C for 1 minute, 46 °C for 50 seconds, and 65 °C for 90 seconds, with a final extension at 65 °C for 10 minutes. PCR products were subjected to agarose gel electrophoresis and purified using a DNA Gel Extraction Kit (CWBiotech, China). The purified products were cloned into the pMD-18T vector (Takara, Japan) and sequenced bidirectionally using an ABI PRISM 3100 automated sequencer (Applied Biosystems, China).

Phylogenetic analysis

Forty myxosporean sequences, including those of the most sequence-similar species and other taxa of interest, were selected for phylogenetic tree construction (Table 1). *Ceratonova shasta* Atkinson, Foott & Bartholomew, 2014 (AF001579) served as the outgroup. The data set was aligned and manually corrected using the Clustal X 1.8 program integrated into MEGA software (Kumar et al. 2018). Phylogenetic relationships were inferred using Bayesian inference (BI) and maximum likelihood (ML) methods (Ronquist et al. 2012; Stamatakis 2014). The optimal evolutionary model for both ML and BI, determined using jModelTest 3.0 under the Akaike information criterion (AIC), was GTR+F+I+G4 (Darriba et al. 2012). Nucleotide frequencies were estimated as A = 0.263, C = 0.199, G = 0.278, and T = 0.260. Nucleotide substitution rates

Table 1. Details of the selected sequences used in the phylogenetic analysis.

Species name	Accession number	Host	Host family/order	Infection tissue	Locality	Source
<i>Myxobolus tachysurus</i> sp. nov.	PP66270	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Palate	China	Present study
<i>Myxobolus voremkhai</i>	KY229919	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Gill	China	GenBank
<i>Myxobolus dumerilii</i>	PP693391	<i>Tachysurus vachellii</i>	Bagridae/Siluriformes	Kidney	China	GenBank
<i>Myxobolus jialingensis</i>	MN066414	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Liver	China	GenBank
<i>Myxobolus xiantaoensis</i>	MT831904	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Fin	China	GenBank
<i>Myxobolus pseudowulii</i>	KY229918	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Skin	China	GenBank
<i>Unicauda pelteobagrus</i>	KC193254	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Muscle	China	GenBank
<i>Myxobolus</i> sp.	JN616264	<i>Leiocassis longirostris</i>	Bagridae/Siluriformes	Gill	China	GenBank
<i>Myxobolus</i> sp.	PP693393	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Skin	China	GenBank
<i>Myxobolus xiushanensis</i>	ON228457	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Gill	China	GenBank
<i>Myxobolus aureus</i>	KF296348	<i>Salminus brasiliensis</i>	Characidae/Characiformes	Liver	Brazil	GenBank
<i>Myxobolus arapiuns</i>	MN239502	<i>Piaractus brachypomus</i>	Characidae/Characiformes	Pyloric cecum	Brazil	GenBank
<i>Myxobolus colossomatis</i>	MK032220	<i>Colossoma macropomum</i>	Characidae/Characiformes	Liver/Pyloric cecum/Gill	Brazil	GenBank
<i>Myxobolus oralis</i>	MF375468	<i>Carassius auratus</i>	Cyprinidae/Cypriniformes	Palate	China	GenBank
<i>Myxobolus hearti</i>	GU574808	<i>Carassius auratus gibelio</i>	Cyprinidae/Cypriniformes	Heart	China	GenBank
<i>Myxobolus pronini</i>	MH329619	<i>Carassius gibelio</i>	Cyprinidae/Cypriniformes	Abdominal cavity	China	GenBank
<i>Myxobolus nielii</i>	JQ690358	<i>Carassius auratus auratus</i>	Cyprinidae/Cypriniformes	Gill	China	GenBank
<i>Myxobolus turpisrotundus</i>	EF690299	<i>Carassius auratus gibelio</i>	Cyprinidae/Cypriniformes	Skin	China	GenBank
<i>Henneguya creplini</i>	EU732597	<i>Zingel zingel</i>	Percidae/Perciformes	Gills	Hungary	GenBank
<i>Henneguya doori</i>	HDU37549	<i>Perca flavescens</i>	Percidae/Perciformes	Gill	USA	GenBank
<i>Henneguya jaczoi</i>	KY172847	<i>Perca fluviatilis</i>	Percidae/Perciformes	Palate	Hungary	GenBank
<i>Henneguya</i> sp.	KY172851	<i>Perca fluviatilis</i>	Percidae/Perciformes	Gill	Hungary	GenBank
<i>Henneguya texta</i>	EU732599	<i>Perca fluviatilis</i>	Percidae/Perciformes	Gill	Hungary	GenBank
<i>Henneguya pungitii</i>	LC544126	<i>Pungitius sinensis</i>	Gasterosteidae/Gasterosteriformes	Skin/Oral mucosa	Japan	GenBank
<i>Myxobolus lepomis</i>	KY203391	<i>Lepomis marginatus</i>	Centrarchidae/Perciformes	Gill	USA	GenBank
<i>Myxobolus polkensis</i>	PQ536837	<i>Lepomis cyanellus</i>	Centrarchidae/Perciformes	Gill	USA	GenBank
<i>Myxobolus khaliiji</i>	KC711053	<i>Acanthopagrus bifasciatus</i>	Sparidae/Perciformes	Intestine	Saudi Arabia	GenBank
<i>Henneguya postexilis</i>	MK811030	<i>Ictalurus punctatus</i>	Ichthyuridae/Siluriformes	Unknown	China	GenBank
<i>Henneguya postexilis</i>	MZ905344	<i>Ictalurus punctatus</i>	Ichthyuridae/Siluriformes	Gill	USA	GenBank
<i>Henneguya ictaluri</i>	AF195510	<i>Ictalurus punctatus</i>	Ichthyuridae/Siluriformes	Gill	USA	GenBank
<i>Henneguya guanduensis</i>	MK415825	<i>Hoplosternum littorale</i>	Callichthyidae/Siluriformes	Gill	Brazil	GenBank
<i>Henneguya</i> sp.	OM158498	<i>Plagioscion squamosissimus</i>	Sciaenidae/Perciformes	Gill	Brazil	GenBank
<i>Henneguya lambariensis</i>	MT952072	<i>Astyanax lacustris</i>	Characidae/Characiformes	Gill	Brazil	GenBank
<i>Myxobolus cultrati</i>	KU170935	<i>Pelecus cultratus</i>	Cyprinidae/Cypriniformes	Eye	Hungary	GenBank
<i>Myxobolus cultus</i>	AB121146	<i>Carassius auratus</i>	Cyprinidae/Cypriniformes	Cartilage	Japan	GenBank
<i>Myxobolus lentisuturalis</i>	OP374272	<i>Carassius auratus</i>	Cyprinidae/Cypriniformes	Muscle	USA	GenBank
<i>Myxobolus branchiopectin</i>	OK274150	<i>Moxostoma duquesnei</i>	Catostomidae/Cypriniformes	Gill	USA	GenBank
<i>Myxobolus separatus</i>	OK012397	<i>Tachysurus fulvidraco</i>	Bagridae/Siluriformes	Gill	China	GenBank
<i>Myxobolus nagaraensis</i>	LC764512	<i>Rhinogobius similis</i>	Gobiidae/Perciformes	Body cavity	Japan	GenBank
<i>Ceratonova shasta</i>	AF001579	<i>Oncorhynchus mykiss</i>	Salmonidae/Salmoniformes	Gallbladder	USA	GenBank

were calculated as follows: AC = 0.84425, AG = 3.25142, AT = 1.47561, CG = 0.44260, CT = 4.47493, and GT = 1.0000. The proportion of invariable sites was 0.268, and the alpha value of the gamma distribution parameter was 0.380. Two independent runs with four chains were conducted for five million generations for BI, with a sampling frequency of 100 and the first 25% of trees discarded as burn-in. Bootstrap support values for ML were calculated from 1000 replications. The resulting phylogenetic tree was visualized using FigTree v1.4.2 (Rambaut et al. 2016) and subsequently edited and annotated using Adobe Illustrator (Adobe Systems Inc., CA).

Results

During sampling, 44 *T. fulvidraco* specimens were dissected to investigate myxosporean infections. Numerous whitish plasmodia were found exclusively in the palate (Fig. 1A), with a prevalence rate of 18.18% (8 of 44). The plasmodia were ellipsoidal in shape, measuring 2.2–3.2 mm in length and 1.1–1.3 mm in width (Fig. 1A, n = 20). No plasmodia or myxospores were detected in other organs, including the intestine, kidney, spleen, skin, and liver. Infected fish exhibited no abnormal symptoms compared with healthy individuals.

***Myxobolus tachysurus* sp. nov.**

<https://zoobank.org/19C4BAB2-9207-4DD8-A069-A0D9E2FD70AE>

Figs 1–4, Table 2, 3

Type host. Yellow catfish, *Tachysurus fulvidraco*

Type locality. Changsha city, Hunan province, China (28°18'58"E, 112°54'4"N).

Site of infection. Palate.

Prevalence. 18.18% (8/44).

Type material. Holotype fixed in 10% formalin was deposited in the Museum of Hydrobiological Sciences, Institute of Hydrobiology, Chinese Academy of Sciences, China (ISB2023122302). Paratypes were fixed in 10% formalin and 95% ethanol, H&E-stained tissue sections, and their digitized photos were deposited in the Museum of Hydrobiological Sciences, Hunan Agricultural University, China (accession numbers HNAU-CF-PAR-25090, HNAU-CF-PAR-25091, HNAU-CF-PAR-25092).

Morphological description. In the valvular view, fresh myxospores are pyriform, whereas in the sutural view, they are fusiform. The myxospores measure 11.4 ± 0.3 (10.8–12.1) μm in length, 7.0 ± 0.2 (6.6–7.4) μm in width, and 5.2 ± 0.3 (4.6–5.8) μm in thickness ($n = 30$). The myxospore surface is smooth, with symmetrically arranged valves. The polar capsules are pyriform and slightly unequal in size. The larger polar capsule measures 6.0 ± 0.3 (5.5–6.6) μm in length and 2.3 ± 0.1 (2.0–2.6) μm in width, whereas the smaller capsule measures 5.4 ± 0.2 (4.9–5.9) μm in length and 2.2 ± 0.1 (1.9–2.4) μm in width ($n = 30$). The polar tube is coiled with six to seven turns. Three to four folds were occasionally observed at the posterior end of the myxospores. Some spores exhibited Henneguya-like caudal appendages. No mucous envelope, iodophilous vacuole, or intercapsular appendix was observed (Figs 1, 2).

Remark. Morphological comparison revealed that eight *Myxobolus* species infecting different sites

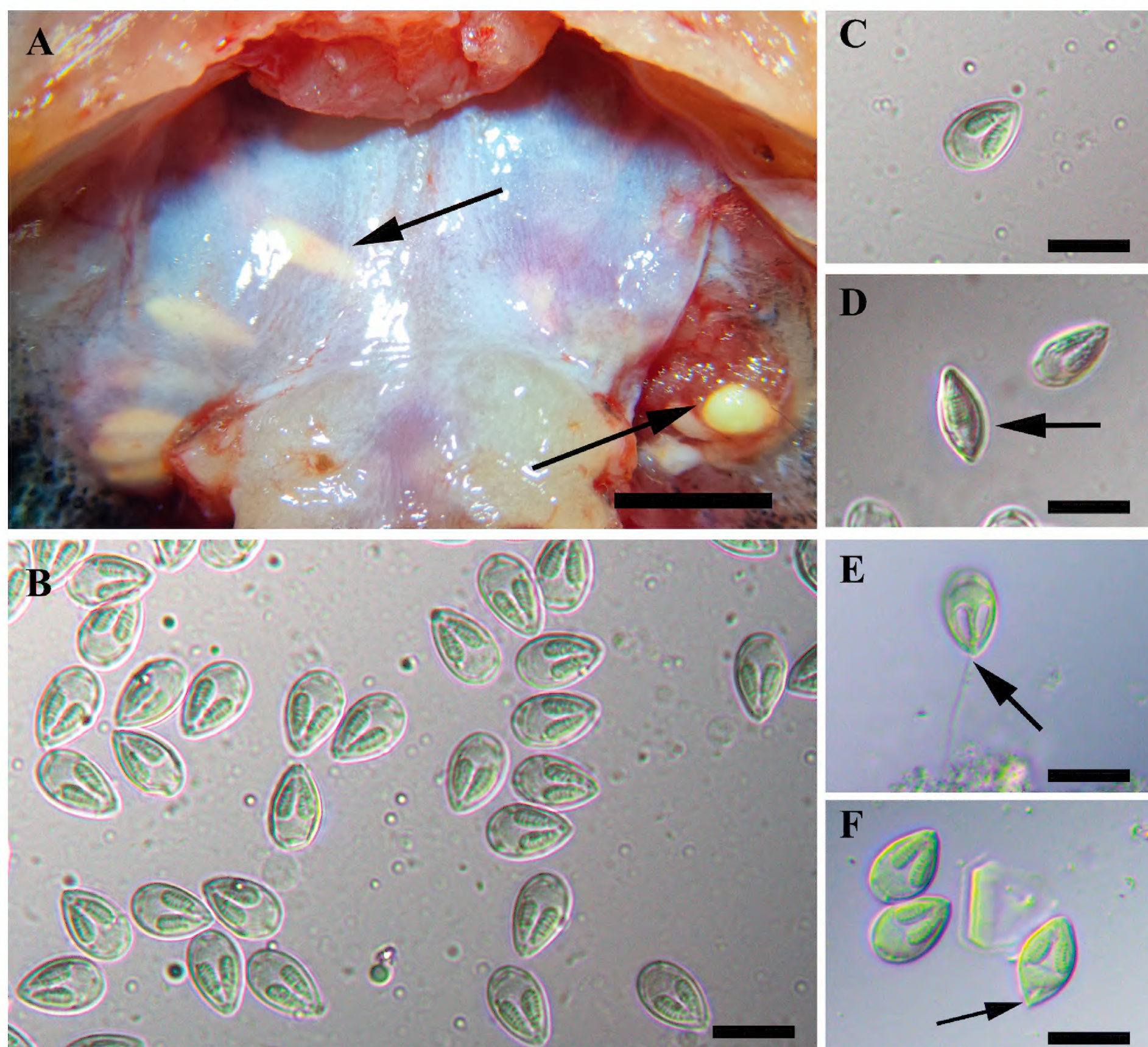


Figure 1. Light microscopic observations of *Myxobolus tachysurus* sp. nov. from *T. fulvidraco*. **A.** Numerous plasmodia within the palate; **B.** Fresh spores; **C.** Myxospore in the valvular view; **D.** Myxospore in the sutural view (arrow); **E.** A myxospore extruding its polar filaments; **F.** An abnormal myxospore with Henneguya-like caudal appendage (arrow). Scale bars: 5 mm (**A**); 10 μm (**B–F**).

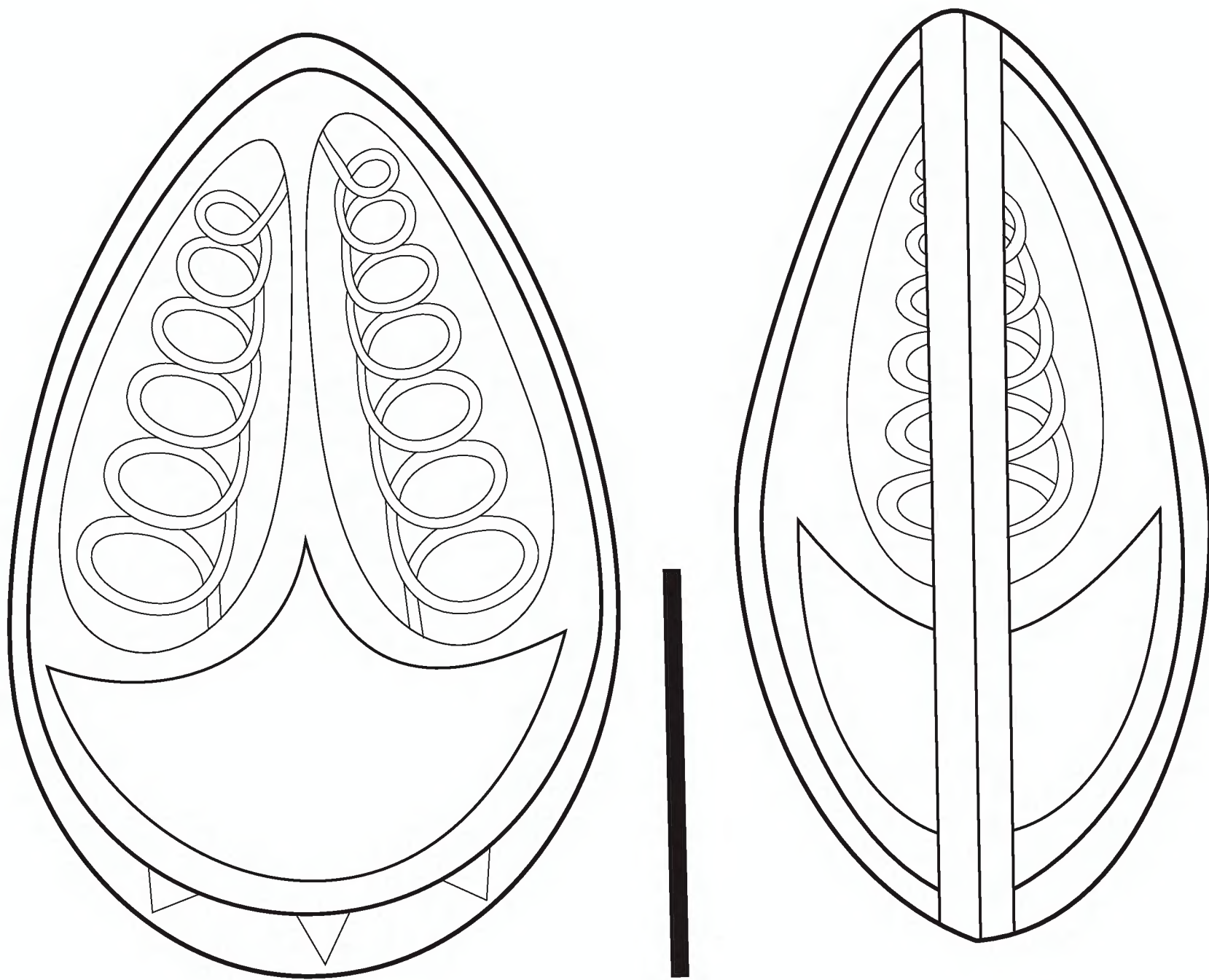


Figure 2. Schematic drawings of *Myxobolus tachysurus* sp. nov. from *T. fulvidraco*. **A.** Myxospore in the valvular view; **B.** Myxospore in the sutural view. Scale bar: 10 μ m.

of *Tachysurus* spp. share the closest morphological resemblance to the new species. These include *Myxobolus xiantaoensis* Tahir, Guo, Zhao, Liu & Gu, 2019; *Myxobolus voremkhai* Akhmerov, 1960; *Myxobolus pseudowulii* Zhang, Zhai, Liu & Gu; *Myxobolus jialingensis* Gao, Zhang, Yang & Zhao, 2020; *Myxobolus macrocapsularis* Reuss, 1906; *Myxobolus physophilus* Reuss, 1906; *Myxobolus vescus* Akhmerov, 1960; and *Myxobolus gigi* Fujita, 1927 (Chen and Ma 1998; Zhang et al. 2017; Tahir et al. 2019; Gao et al. 2020; Zhang et al. 2025) (Table 2). Among them, *M. xiantaoensis*, *M. voremkhai*, *M. pseudowulii*, and *M. jialingensis* resemble the new species due to their slightly unequal polar capsules. However, these species can be distinguished from the new species by their larger myxospore size, different infection sites, the presence of membrane sheaths, and larger polar capsules (Zhang et al. 2017; Tahir et al. 2019; Gao et al. 2020; Zhang et al. 2025). In addition, *M. pseudowulii* and *M. jialingensis* differ from *M. tachysurus* sp. nov. by having slightly more polar tube turns (7–9 vs. 6–7). The present species produces relatively large cysts (2.2–3.2 mm $\times$ 1.1–1.3 mm), which are smaller than those of *M. jialingensis* (3.1 $\times$ 2.8 mm) but larger than those of *M. voremkhai* (0.86 mm in diameter) and *M. pseudowulii* (0.65–1.09 mm in diameter). *Myxobolus macrocapsularis*, *M. physophilus*, *M. vescus*, and

M. gigi, all characterized by equal polar capsules, were described in the last century (Chen and Ma 1998). *Myxobolus macrocapsularis* and *M. physophilus* differ from the present species by the presence of a distinct intercapsular appendix at the anterior end and a slightly greater spore length. Furthermore, *M. physophilus* is further distinguished from the novel species by a higher number of posterior folds (5–6 vs. 3–4), broader spore width (8.4–9.6 μ m vs. 6.6–7.4 μ m), greater spore thickness (8.4 μ m vs. 4.6–5.8 μ m), and different infection sites. *Myxobolus vescus*, which infects the stomach and kidney of *T. fulvidraco* and the gills of *T. vachellii*, differs by having a smaller spore width and thickness (4.8–6.3 μ m $\times$ 3.1–3.8 μ m vs. 6.6–7.4 μ m $\times$ 4.6–5.8 μ m) and slightly more polar tube turns (7–8 vs. 6–7). *Myxobolus gigi* differs from *M. tachysurus* sp. nov. by its much smaller plasmodia (22 μ m in diameter vs. 2.2–3.2 mm $\times$ 1.1–1.3 mm), larger spore length (12.0–14.4 μ m vs. 10.8–12.1 μ m), and absence of posterior folds.

Histopathology. Histological analysis revealed that the plasmodia of the new species were located within the muscle layer of the palate (Fig. 3). The plasmodium was encapsulated by a layer of connective tissue, in which immature myxospores were found peripherally, whereas mature myxospores were situated centrally (Fig. 3). No inflammatory response was observed.

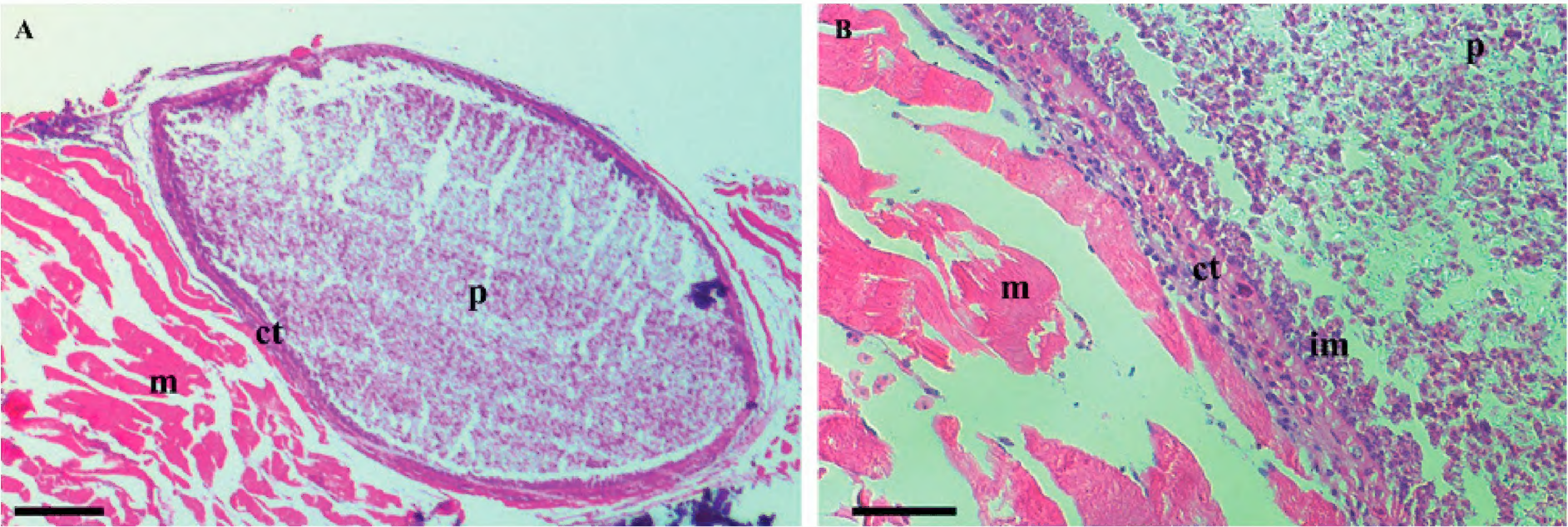


Figure 3. Histopathological analysis of the palate of *T. fulvidraco* infected with *Myxobolus tachysurus* sp. nov. **A.** Plasmodium (p) surrounded by connective tissue (ct), located in the muscle layer (m) of the palate; **B.** Magnified view of the plasmodium in Fig. 3A, showing the plasmodium surrounded by connective tissue (ct), with mature spores located centrally and immature spores (im) peripherally. Scale bar: 300 μ m (**A**); 50 μ m (**B**).

Table 2. Comparison of *Myxobolus fulvidraco* sp. nov. with the most morphologically similar *Myxobolus* species.

Species	LS	WS	TS	LPC	WPC	PF	H	IF	Ref
<i>M. tachysurus</i> sp. nov.	11.4 $\pm$ 0.3 ^a (10.8–12.1) ^b	7.0 $\pm$ 0.2 (6.6–7.4)	5.2 $\pm$ 0.3 (4.6–5.8)	6.0 $\pm$ 0.3 (5.5–6.6) 5.4 $\pm$ 0.2 (4.9–5.9)	2.3 $\pm$ 0.1 (2.0–2.6) 2.2 $\pm$ 0.1 (1.9–2.4)	6–7	<i>T. fulvidraco</i>	Palate	Present study
<i>M. xiantaoensis</i>	12.6 $\pm$ 0.6 (11.3–13.9)	9.6 $\pm$ 0.6 (8.4–11.1)	7.1 $\pm$ 0.4 (6.1–7.7)	6.8 $\pm$ 0.5 (6.0–8.1); 6.4 $\pm$ 0.3 (5.5–7.4)	3.4 $\pm$ 0.2 (3.0–3.8) 3.6 $\pm$ 0.2 (3.2–3.9)	6–8	<i>T. fulvidraco</i>	Fins	Tahir et al. (2019)
<i>M. voremkhai</i>	14.5 $\pm$ 0.5 (13.1–15.5)	7.8 $\pm$ 0.3 (7.1–8.6)	6.3 $\pm$ 0.4 (5.6–7.2)	6.8 $\pm$ 0.3 (6.3–7.4); 6.5 $\pm$ 0.3 (5.8–7.1)	2.8 $\pm$ 0.2 (2.2–3.3); 2.8 $\pm$ 0.2 (2.2–3.3)	5–7	<i>T. fulvidraco</i>	Gills	Zhang et al. (2017)
<i>M. pseudowulii</i>	14.6 $\pm$ 0.7 (12.9–16.2)	9.4 $\pm$ 0.5 (8.1–10.8)	7.0 $\pm$ 0.4 (6.1–8.1)	7.9 $\pm$ 0.4 (7.2–9.5); 7.4 $\pm$ 0.3 (6.9–8.0)	3.5 $\pm$ 0.2 (3.0–3.9) 3.4 $\pm$ 0.2 (2.9–3.9)	7–9	<i>T. fulvidraco</i>	Skin	Zhang et al. (2017)
<i>M. jialingensis</i>	15.8 $\pm$ 0.7 (15.4–17)	8.0 $\pm$ 0.3 (7.9–8.9)	–	7.4 $\pm$ 0.3 (6.7–8.0); 7.3 $\pm$ 0.3 (6.6–8.1)	3.1 $\pm$ 0.2(2.8–3.6); 3.3 $\pm$ 0.2 (2.9–3.6)	7–8	<i>T. fulvidraco</i>	UB ^d	Gao et al. (2020)
<i>M. macrocapsularis</i>	12.1 (12.0–12.6)	7.2 (6.6–7.6)	6.1 (6.0–6.2)	5.7 (5.4–6.0)	2.1 (2.2–2.4)	7–8	<i>T. fulvidraco</i>	Kidney, intestine, UB	Chen and Ma (1998)
<i>M. physophilus</i>	12.5 (12.0–13.0)	9.0 (8.4–9.6)	8.4	7.2 (6.6–8.4)	3.1 (2.8–3.6)	6–7	<i>T. fulvidraco</i> , <i>T. nitidus</i>	Gills, kidney, UB, fins	Chen and Ma (1998)
<i>M. vascus</i>	10.1 (8.6–11.2)	5.6 (4.8–6.3)	3.3 (3.1–3.8)	5.1 (4.4–5.6)	1.2 (1.0–1.4)	7–8	<i>T. fulvidraco</i> <i>T. vachellii</i>	Gills, kidney, stomach	Chen and Ma (1998)
<i>M. gigi</i>	13.6 (12.0–14.4)	7.4 (7.2–8.4)	5.9 (5.8–6.0)	7.4 (7.0–7.8)	2.9 (2.4–3.6)	6–7	<i>T. fulvidraco</i>	Gills	Chen and Ma (1998)

All measurements are in micrometers (μ m). LS, length of the spore; WS, width of the spore; TS, thickness of the spore; LPC, length of the polar capsule; WPC, width of the polar capsule; CPF, number of coils of the polar filament; FV, spore shape in the frontal view; H, host; IF, infection sites; Ref., references.

^a Mean $\pm$ SD; ^b Minimum–maximum; ^c Mean; ^d Urinary bladder and hepatopancreas.

Molecular characterization. BLASTn analysis demonstrated that the obtained sequence of *M. tachysurus* sp. nov. did not match any sequences available in GenBank but was most closely related to *Myxobolus separatus* Zhang & Gu, 2021 (95.82%, [OK012397](#)), which infects the gill filaments of *T. fulvidraco*. Other sequences showing notable similarity include *Myxobolus nagaraensis* Yokoyama, Kageyama, Ohara & Yanagida, 2007 (89.82%, [LC764514](#)), isolated from the visceral cavities of gobies *Rhinogobius fluviatilis* Tanaka, 1925; *Myxobolus lentisuturalis* Dyková, Fiala & Nie, 2002 (89.62%, [QR416134](#)) from the muscle of the Prussian carp *Carassius gibelio*; *Myxobolus* sp. (89.59%, [KU170935](#)) from the retinal layer of the eyes of *Pelecus cultratus* Linnaeus, 1758; *Myxobolus branchiopectin* Ksepka & Bullard, 2021 (89.48%, [OK274150](#)) from the cartilage of the gill raker of *Moxostoma duquesnii* Lesueur, 1817; and

Myxobolus cultus Yokoyama, Ogawa & Wakabayashi, 1995 (89.50%, [KY784599](#)) from the cartilage of goldfish *Carassius auratus*. The genetic distances and sequences similarities calculated using Kimura 2-parameter model among the present species and those with high sequence similarity ranged from 0.114/95.82% to 0.286/82% (Table 3). Phylogenetic analysis indicated that the generated trees were resolved into four major clades (Clades A–D), and species were clustered mainly according to host affinity, with some exceptions, rather than infection sites or host locality (Fig. 4). The present species did not cluster with *T. fulvidraco*–infecting *Myxobolus* species within Clade D but formed a sister clade to *M. separatus*, infecting the gill filaments of *T. fulvidraco*, and *M. nagaraensis* within Clade A, with moderate support values (Fig. 4).

Etymology. The species is named after the generic name of the host.

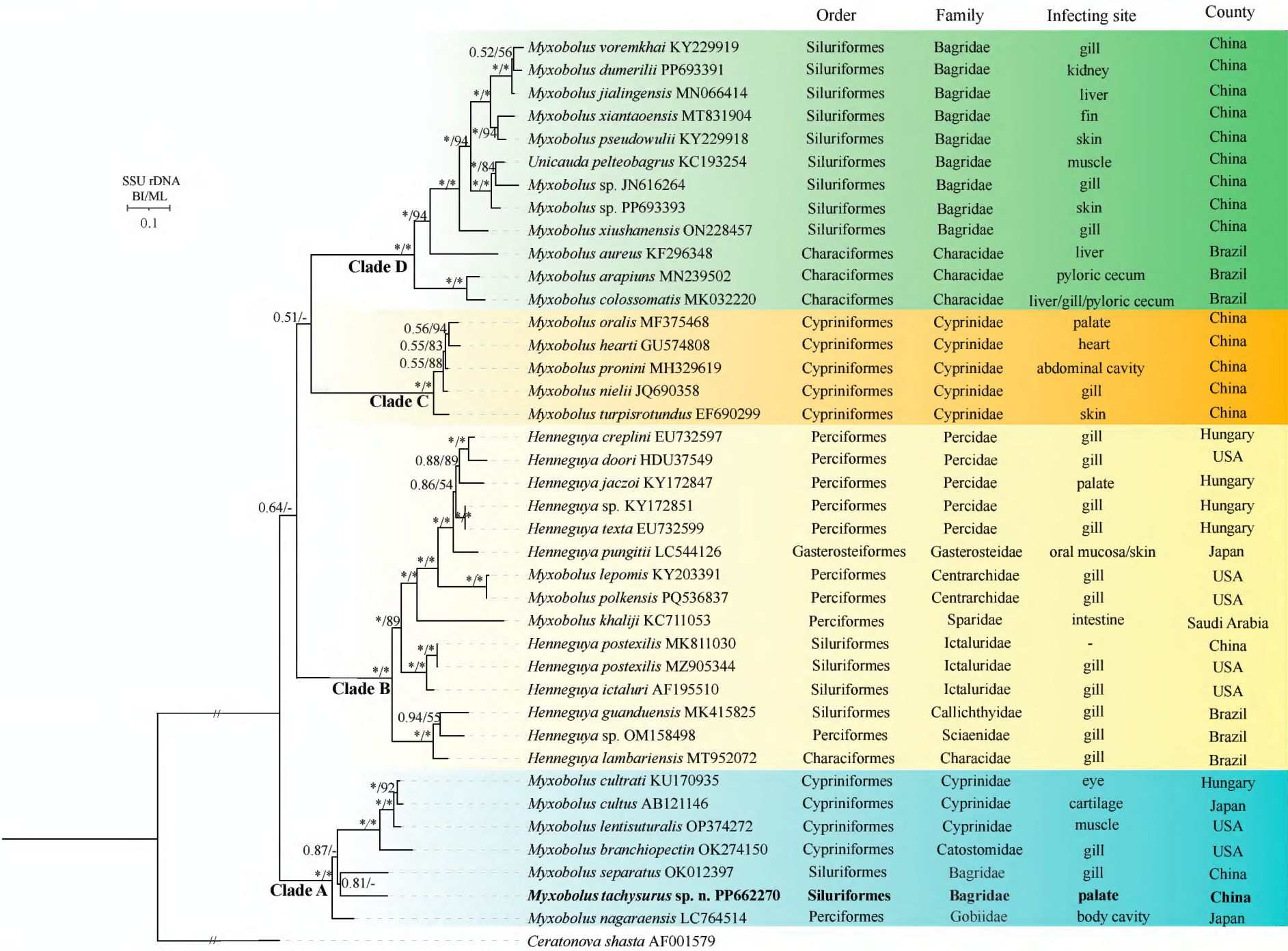


Figure 4. Phylogenetic tree of *Myxobolus tachysurus* sp. nov. and related species based on SSU rDNA sequences, rooted with *Ceratonova shasta*. Support values at branch nodes are shown as BI posterior probabilities/ML support values; asterisks indicate support values > 0.95 or 95%, and dashes indicate support values < 0.50 or 50%.

Table 3. Comparison of sequence similarities (upper right) and genetic distances (lower left) between *Myxobolus tachysurus* sp. nov. and other genetically related or morphologically similar *Myxobolus* species based on partial 18S rDNA.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>M. tachysurus</i> sp. nov. PP662270		95.82	89.82	89.62	89.59	89.48	89.50	85.2	81.72	81.84	84.71	85.79	82.00
2 <i>M. separatus</i> OK012397	0.114		94.3	88.55	88.50	88.03	88.33	87.78	86.78	87.74	88.14	90.00	87.71
3 <i>M. nagaraensis</i> LC764514	0.128	0.134		86.28	85.54	87.86	86.13	83.29	79.93	80.66	84.27	84.83	83.70
4 <i>M. lentisuturalis</i> OP374272	0.136	0.140	0.150		95.76	90.45	95.86	84.42	84.12	84.88	85.24	86.45	84.92
5 <i>Myxobolus</i> sp. KU170935	0.138	0.147	0.155	0.020		89.70	96.97	84.07	80.72	81.04	84.82	85.87	84.40
6 <i>M. branchiopectin</i> OK274150	0.155	0.153	0.160	0.089	0.086		90.33	82.43	81.60	83.45	83.91	85.37	83.36
7 <i>M. cultus</i> KY784599	0.143	0.150	0.154	0.030	0.013	0.093		83.75	80.88	80.25	84.51	86..52	84.23
8 <i>M. jialingensis</i> MN066414	0.270	0.292	0.297	0.274	0.273	0.289	0.272		96.24	90.69	88.48	84.19	91.94
9 <i>M. voremkhai</i> KY229919	0.279	0.294	0.298	0.284	0.285	0.290	0.283	0.036		91.16	87.72	82.87	91.83
10 <i>M. xiantaoensis</i> MT831904	0.284	0.290	0.304	0.289	0.289	0.293	0.291	0.090	0.091		88.60	83.08	94.70
11 <i>M. xiushanensis</i> ON228457	0.289	0.297	0.310	0.283	0.282	0.290	0.285	0.115	0.123	0.123		83.77	89.28
12 <i>M. oralis</i> MF375468	0.265	0.275	0.263	0.266	0.271	0.266	0.271	0.278	0.286	0.294	0.274		82.92
13 <i>M. pseudowulii</i> KY229918	0.286	0.295	0.303	0.284	0.288	0.306	0.290	0.079	0.087	0.055	0.106	0.290	

Discussion

The yellow catfish (*T. fulvidraco*) is an economically significant freshwater fish, widely distributed across rivers, lakes, and ponds in China. Due to its desirable taste and high nutritional value, it is extensively farmed across numerous provinces in China. In 2023, annual production in

China reached up to 623 thousand metric tons (Liu, 2024). Intensive aquaculture practices in China have led to outbreaks of various diseases, including “Ulcerative Disease Syndrome” (Liu et al. 2023), “Hole in Head Disease” (Hu 2022), and “Ascites Disease” (Xu et al. 2009; Yang et al. 2019), causing severe damage to the yellow catfish industry and resulting in substantial losses for fish farmers.

Myxosporidiosis has become a frequent and serious parasitic disease in yellow catfish (Zhang et al. 2017; Tahir et al. 2019; Gao et al. 2020; Zhang et al. 2025). Currently, more than 30 species have been identified from various organs of yellow catfish (Chen and Ma 1998; Zhang et al. 2017; Tahir et al. 2019; Gao et al. 2020; Zhang et al. 2025). While most are harmless to the host, certain species can cause significant mortality. Notable among these are the newly identified *Sphaerospora fulvidraco* Zhang, Zheng & Yin, 2026, infecting renal tissues; *Myxobolus xiantaoensis* Tahir, Guo, Zhao, Liu & Gu, 2019, affecting the fins; and *Myxobolus pseudowulii* Zhang, Zhai, Liu & Gu, 2017, targeting the skin (Zhang et al. 2017; Tahir et al. 2019; Gao et al. 2020; Zhang et al. 2025).

The palate is an uncommon site for myxosporean infections, with only two *Myxobolus* species recorded previously: *Myxobolus peachiformis* Ma, 1998, from *Zacco platypus* Jordan & Evermann, 1902, and *Myxobolus oralis* Whipps, Nie & Gu, 2014, from *C. auratus gibelio* (Chen and Ma 1998; Liu et al. 2014). *Myxobolus peachiformis* can be readily distinguished from the new species by its equal-sized polar capsules, larger spores ($15.6\text{--}16.3\ \mu\text{m} \times 11.4\text{--}13.0\ \mu\text{m} \times 8.1\text{--}8.4\ \mu\text{m}$ vs. $10.8\text{--}12.1\ \mu\text{m} \times 6.6\text{--}7.4\ \mu\text{m} \times 4.6\text{--}5.8\ \mu\text{m}$) and polar capsules ($7.5\text{--}8.4\ \mu\text{m} \times 3.8\text{--}4.2\ \mu\text{m}$ vs. $4.9\text{--}6.6\ \mu\text{m} \times 1.9\text{--}2.6\ \mu\text{m}$), as well as a different host (*Z. platypus*, belonging to Cypriniformes) (Chen and Ma 1998). *Myxobolus oralis* differs from the new species by its distinct spore shape (obovate vs. pyriform), equal polar capsules, and greater spore width ($8.2\text{--}9.9\ \mu\text{m}$ vs. $6.6\text{--}7.4\ \mu\text{m}$) (Liu et al. 2014). The low sequence similarity (85.79%) and distinct clade placement (*M. oralis* within Clade C and *M. tachysurus* sp. nov. within Clade A, as shown in Fig. 4) within the phylogenetic tree further support the conclusion that these represent two distinct species.

Phylogenetic analysis indicated that the selected species primarily clustered based on host affinity, although some exceptions have been reported previously (Liu et al. 2019; Zhao et al. 2023; Zhao et al. 2024). Notably, the new species did not cluster with Siluriformes-infecting species with pyriform myxospores within Clade D but formed a sister group to *M. separatus* within Clade A. This finding further supports the assertion that phylogenetic host affinity provides a stronger evolutionary signal than myxospore morphology, consistent with previous research (Wu et al. 2019). Infection-site tropism is a significant characteristic in myxozoan taxonomy. Korean researchers demonstrated a correlation between infection-site tropism and Myxobolidae phylogeny, categorizing species into specific infection-site tropism groups (primarily gill- and muscle-infecting species) and non-specific infection-site tropism groups (species infecting gills, intestine, skin, swim bladder, and fins) (Shin et al. 2014). The present species appears to belong to the non-specific infection-site tropism group, as species within Clade A originate from diverse infection sites.

Although geographic distribution has been implicated in the phylogenetic structuring of myxozoans (Zhao et al.

2024; Velasco et al. 2024; Xiong et al. 2025), the present analysis reveals a limited discernible phylogenetic signal for this factor. This conclusion is supported by the observation that individual clades, such as Clades A and B, comprise species collected from multiple, widely separated countries. The phylogeny generated herein was predominantly shaped by host affinity, with neither infection site nor geographic distribution appearing to be a major determinant of topology. Further research is required to elucidate the potential contributions of these ecological and geographic variables to myxozoan evolution.

Conclusion

In summary, the new species *Myxobolus tachysurus* sp. nov., infecting the palate of *T. fulvidraco*, is comprehensively described based on morphological, ecological, and molecular data.

Acknowledgements

This work was supported by the Natural Sciences Foundation of China (32100364), the Earmarked Fund for HARS (HARS-07), the Natural Sciences Foundation of Hunan (2024JJ6241), and the Hunan Provincial Education Department (23B0211).

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